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COMPARATIVE LIFE HISTORY AND RESPIRATORY ACTIVITY OF "WILD" AND COLONIZED CARIBBEAN FRUIT FLIES [*DIPT.: TEPHRITIDAE*] (1)

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Insects that are colonized for use in biological control programs must be behaviorally functional with respect to target field populations. To quantify adaptation during colonization and identify some of the behavioral changes that occur during the process, comparable colonies of field-collected and laboratory-adapted Caribbean fruit flies, *Anastrepha suspensa* (LOEW), were monitored through 5 generations for fertility of eggs, weights and yields of pupae, and viability, sex ratio, insemination frequency, fecundity, and CO^2 production of adults. After five generations, the wild strain still produced 57 % fewer eggs, required 6-7 extra days per cycle (16 % longer), and produced 16 % less CO^2 per generation.

Historically, the objective of insect colonization has been the efficient production of a required quantity and stage of a particular species; quality has been assumed. More recent biological control strategies, however, have necessitated the rearing of behaviorally competitive strains. To achieve this goal, a compromise has been necessary between the physical contraints involved in rearing programs and the behavioral capabilities of resulting insects (CHAMBERS, 1975). Consequently, behavior of field-released insects has become a primary consideration that must be studied systematically and understood throughly to insure successful performance (BOLLER, 1972).

Determination of minimum standards for insect quality depends on the specific objectives of the individual control program (MACKAUER, 1972). These standards may be achieved by identifying and managing the various selective forces that occur during colonization. Selection for characteristics amenable to laboratory environments is presumed to occur through rapid "bottleneck" effects (BOLLER, 1972) and as a result of adaptation over many generations. Thus, undefined environmental conditioning (non-genetic) and genetic divergence of cultured strains from "wild" populations have become fundamental considerations in the concept of quality control in insect rearing.

We selected the Caribbean fruit fly, *Anastrepha suspensa* (LOEW), (*Dipt.: Tephritidae*) for an experimental insect and studied some of the adaptive processes that occur during colonization of this species. Our objective was to record the development of

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each stage of the life cycle of a field-collected (wild) population that was being colonized and compare this wild colony with an established laboratory strain. Overall viability, fertility, fecundity, rate of development, and carbon dioxide produced by adults were used to monitor relative adaptedness.

MATERIALS AND METHODS

The laboratory strain was established with about 2000 pupae supplied by R.M. BARANOWSKI (University of Florida) from a colony maintained for more than 4 years (ca. 35 generations) at Homestead, Fla. (KAMASAKI *et al.*, 1970). The wild population of 1882 pupae was obtained from infested common guava, *Psidium guajava* L., that were collected from the Homestead area. Subsequently, equivalent colonies of both strains were reared according to standard procedures (BURDITT *et al.*, 1974) for 5 generations at Gainesville, Fla. Larvae were fed 200 g of bagasse diet (GREANY *et al.*, 1975) per 200-7000 eggs, depending on the rate of oviposition. Pupation occurred in moist vermiculite (113-2205 pupae/40 g) and approximately 2000 pupae of each strain were transferred to separate 31-cm^3 wire screen cages for emergence. Adults were provided with moisture and a food strip made of a brown sugar and yeast hydrolysate paste applied to a paper backing (PROKOPY & BOLLER, 1970). The rear panel of each cage was lined with cheese cloth impregnated with a 2:1 mixture of red paraffin and petroleum jelly to provide an oviposition substrate. Fresh provisions were added to the cage weekly, and the colonies were maintained at 27 ± 1°C and $65\pm5\%$ RH with a 14-hr photophase (310-750 nm, 17-29 ft-c).

Eggs were collected from each cage daily, measured volumetrically, subsampled for percentage hatch (100 eggs), and incubated or discarded. Duration of the larval stage, mean pupal weight and yield, and number, sex, and insemination frequency of emergent adults were also recorded. Only eggs deposited during peak oviposition (day 12-18 postemergence) and pupae from the period of peak pupation (days 14-17 post-oviposition) were used to establish subsequent generations. Daily records were accumulated for each generation of both strains, averaged, and converted arithmetically to relative percentages for the analyses. Significant differences in life history parameters were determined by applying Student's *t*-test at the 5% level of probability to the differences between these values. The percentages were convenient but occasionally misleading; therefore numerical data also are reported for clarification.

The 24 hr production of CO_2 by 11 day-old flies served as an index of physical activity for successive generations (F_2, F_3, and F_5) of both strains. After a one-day adaptation period, 50 pairs of flies were confined in a 0.012 m^3 plexiglass box and monitored for 24 hr with a CO_2 sensing device (TURNER & CHARITY, 1971). A cam-operated shutter produced gradual transitions during the 13L:11D photoperiod, and light intensities of 0.003 to 50 ft-c were produced by four 20W cool white lamps. A Photovolt 502 M Photometer was used to calibrate the system. Initially, behavioral responses were analyzed in terms of total activity (CO_2 discharged), thresholds (changes relative to light intensity), startle (immediate changes during phase transitions), and general patterns (shape of the 24 hr-curves).

RESULTS AND DISCUSSION

Through the F_5 generation, mean egg fertility ($56\pm24\%$), pupal weight (12.7 ± 1.7 mg) and yield ($10\pm6\%$), and adult emergence ($94\pm4\%$), sex ratio (50-30%

TABLE 1

Comparison of the laboratory life histories of wild and colonized strains of the Caribbean fruit fly, Anastrepha suspensa

Generation	*Relative percentage of performance* (a)				
	Eggs deposited	Eggs hatched	Pupal yields	Pupal weights	Generation time
P_1	< 5	> 90	--	94.3	--
F_1	< 5	91.5	107.9	119.0	116.2
F_2	7.8	57.8	> 95	> 95	113.3
F_3	26.3	100.0	103.7	90.1	115.8
F_4	18.7	80.9	60.6	103.5	120.0
F_5	43.2	72.2	76.6	104.5	116.2

(a) Indicates wild relative to laboratory strain, entries with signs are estimates.

males vs. 50-70% females), and insemination frequency (43±6% mated females) were statistically equivalent for the two strains (table 1). GREANY *et al.* (1976), by using comparable rearing protocols, achieved an average pupal weight of 13.2±0.2 mg and 99±1% adult emergence. Thus, these criteria were relatively independent of selection during colonization.

Wild strain females consistently oviposited nearly 57% fewer eggs than the laboratory strain (138 and 320 eggs/mated female, respectively). The wild strain also required 42-45 days to complete each generation, whereas the colonized flies cycled every 35-38 days. There was no appreciable difference in the time required for eggs of the two strains to develop; however, a 2-day delay in larval development, a 4- to 5-day extension of the preoviposition period, and reduced fecundity indicated a general lack of adaptation by the wild strain to the laboratory environment. KAMASAKI *et al.* (1970) also observed prolonged preoviposition and reduced fecundity during the original colonization of *A. suspensa*, and noted that the oriental fruit fly, *Dacus dorsalis* HENDEL, adapted progressively through 10 generations. However, the Mediterranean fruit fly, *Ceratitis capitata* (WEIDEMANN), has reportedly attained appreciable levels of adaptation to the insectary within 5 generations (ROSSLER, 1975b). In that study, the preoviposition period of F_{12} colonized females remained 1-2 days longer than for a 12-year-old colony, but the egg viability and patterns of reproduction were equivalent. ROSSLER (1975a) crossed field-collected females with males from the established colony and reported that 41% of the females remained unmated. The other 3 homo- and heterogamic crosses yielded 92-97% mated females. Similar results were obtained with *Culex nigripalpus* THEOBALD, and the F_1 progeny from wild males X colony females were actually laboratory adapted (HAEGER & O'MEARA, 1970). Apparently, acceptance of confinement, artificial provisions, the oviposition substrate, and other "unnatural" environmental stimuli are critical factors particularly for colonization of females of certain fruit flies and mosquitoes.

Patterns of CO_2 output were generally similar for both strains (fig. 1). Diurnal CO_2 production was 74.2, 76.6 and 54.9 cc for the wild type and 83.8, 102.4 and 62.3 cc for the laboratory strain during the F_2, F_3 and F_5 generations, respectively. The respective nocturnal values were 43.0, 42.7 and 29.6 cc; 45.1, 54.9 and 34.1 cc. Thus, laboratory flies had a maximum of 39% and wild type 29% difference in total CO_2 production between generations; however, differences between strains for a single generation ranged from only 9 to 24%. During the 24-hr cycle an average of approximately 16% more CO_2

was produced by the laboratory flies than by the wild strain, and this elevated CO_2 output was similar in average magnitude to the shorter development time for the laboratory flies.

Changes in diel periodicity and thresholds of response to light intensity during phase transitions indicated some adaptation of the wild strain to insectary lighting within 5 generations. At the onset of each photophase, activity (CO_2 production) was initiated for all generations of both strains when the light intensity was below 0.1 ft-c.; however, differences occurred during the diurnal to nocturnal change of phase. Activity of the F_2 wild-type decreased at 1.0 ft-c.; the response threshold occurred 10 min earlier, at 1.5 ft-c., in the laboratory strain. Subsequent generations of both strains responded at 1.5 ft-c.

The ratio of diurnal to nocturnal CO_2 averaged 1.85 for the laboratory strain and increased from 1.73 in the F_2 to 1.86 in the F_5 wild flies. In addition, the number of short flights, apparently random spikes on the CO_2 record produced by the F_3 laboratory strain, indicated that these flies were more irritable than the other test populations. Conversely, both F_5 populations were exceptionally quiescent. Patterns of activity were similar but not identical for either strain during any generation. General patterns of respiration therefore indicated the relative adaptedness of these strains in the laboratory, but did not identify the specific physiological and behavioral differences.

If, as MACKAUER (1972) & ROSSLER (1975a) emphasized, characters that contribute optimal fitness in the insectary will be ineffectual under field conditions, then alteration of essential behavior must be avoided during colonization. In our study, the wild flies were assumed to originate from the same parent population as the colonized strain, but as a precaution against excessive selection, eggs and pupae for subsequent generations were recovered during the median period for completion of each stage. The relatively small population sizes and somewhat modified rearing protocols, however, would be expected to yield differences between the strains. Fluctuations in moisture content of the larval medium and an absence of natural sensory stimuli in the adult cage environment actually prevented either strain from achieving adaptive stabilization. Ultimately, egg to adult yields of about 10% for both colonies indicated establishment of low-level production equilibria and intense selection (bottleneck) for insects capable of accepting the laboratory environment.

The pragmatic questions concerning insect colonization are: how does the evolution of a domestic population that results from selective forces imposed by man differ from that of the target population; and how may the contributing factors be managed? To solve these problems, specific behavioral traits that determine fitness and, therefore, survival of a useful species in an appropriate environmental context must be identified and rated. A dynamic standard of insect quality would result from repeated evaluation of insect performance and "feedback" of this information into the rearing process. This standard would be based on subjective evaluations of the relative performance of a set of essential behavior patterns by the colonized strain. By adopting this system, species could be mass produced according to actual program criteria and would thus become functionally successful in insect control. In our initial research, we used physiological criteria as indices of relative fitness for the Caribbean fruit fly, and indirectly measured some of the behavioral components of insect quality.

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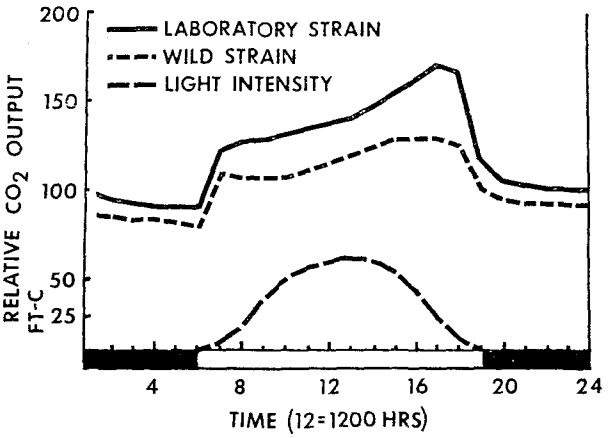

FIG. 1. Average carbon dioxide production recorded from 11-day-old populations of 50 pairs of F_2, F_3 and F_5 laboratory and wild type Caribbean fruit flies (cc CO_2/min per 100 pairs = 0.00006 X ordinate value ± 15 %); and hourly transitions in light intensity.

RÉSUMÉ

Comparaison de la biologie et de l'activité respiratoire de mouchés antillaises des fruits sauvages et d'élevage [*Dipt. : Tephritidae*]

Les insectes élevés au laboratoire et destinés à être utilisés dans des programmes de lutte biologique doivent présenter des comportements similaires à ceux des insectes sauvages. De façon à étudier les modifications de comportement ainsi que les adaptations aux conditions d'élevage, deux souches de la Mouche antillaise des fruits *Anastrepha suspensa* (LOEW) ont été comparées. L'une recueillie dans la nature et l'autre adaptée aux conditions d'élevage ont été suivies pendant 5 générations au cours desquelles ont été étudiés la fertilité des œufs, le poids et le nombre de pupes formées, la longévité, le sex-ratio, la fréquence des accouplements, la fécondité et la production de CO_2 chez les insectes parfaits. Pendant les 5 générations les insectes issus de la nature ont présenté par rapport aux insectes d'élevage une fécondité réduite de 51 %, une durée de développement supérieure de 16 % et une production de CO_2 pendant la photophase diminuée de 16 %.

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